

MARINE MAMMAL SCIENCE, 24(4): 815–830 (October 2008)
© 2008 by the Society for Marine Mammalogy
DOI: 10.1111/j.1748-7692.2008.00217.x

Migratory movements and surfacing rates of humpback whales (*Megaptera novaeangliae*) satellite tagged at Socorro Island, Mexico

BARBARA A. LAGERQUIST

BRUCE R. MATE

JOEL G. ORTEGA-ORTIZ

MARTHA WINSOR

Department of Fisheries and Wildlife,
Coastal Oregon Experiment Station,
Oregon State University,
Hatfield Marine Science Center,
Newport, Oregon 97365, U.S.A.
E-mail: barb.lagerquist@oregonstate.edu

JORGE URBÁN-RAMIREZ

Departamento de Biología Marina,
Universidad Autónoma de Baja California Sur,
Ap. Post 19-B, La Paz, B. C. S. 23081, Mexico

ABSTRACT

Humpback whales wintering in the Revillagigedo Archipelago, Mexico, have been considered a different subpopulation from those found off mainland Mexico and Baja California. The primary feeding grounds for Revillagigedo humpbacks remain unknown. In February 2003, we deployed 11 Argos satellite-monitored radio tags to track movements and surfacings of humpback whales (five adults without calves, five mothers with calves, one calf) off Socorro Island in the Revillagigedo Archipelago. Tracking ranged from 222 to 10,481 km over 4.9–149.1 d. Eight whales left Socorro Island: five visited other Mexican wintering destinations, seven moved north of these areas. Migration routes were primarily offshore (average 444 km). Two whales were tracked to feeding grounds: one to British Columbia (46 d migration), and one to Alaska (49 d migration). Mean travel speeds were 1.2 km/h in wintering areas, 4.0 km/h during migration, and 2.2 km/h in feeding areas. Overall surfacing rates ranged from 21 to 88 surfacings/h. Surfacing rates differed between the calf and all other whales, and between feeding areas and migratory/wintering areas for the calf and an adult without a calf. The calf also showed diel variation in surfacing rates. The offshore habits of tagged whales may explain scarce resightings of Revillagigedo humpbacks outside the Revillagigedo Archipelago.

Key words: humpback whale, *Megaptera novaeangliae*, migration, satellite telemetry, Revillagigedo Archipelago, Alaska, British Columbia.

There is evidence for at least three subpopulations or stocks of humpback whales in the North Pacific (Calambokidis *et al.* 2001): the western North Pacific stock, wintering in the Ogasawara and Ryukyu Islands of Japan and possibly summering in the waters west of the Kodiak Archipelago (Nishiwaki 1966, Calambokidis *et al.* 2001); the central North Pacific stock, wintering in the Hawaiian Islands and summering in northern British Columbia/Southeast Alaska and Prince William Sound west to Kodiak (Baker *et al.* 1998, Calambokidis *et al.* 2001); and the eastern North Pacific stock, wintering in the waters of Mexico and Central America and summering in California, Oregon, Washington, British Columbia, and Alaska (Baker *et al.* 1998, Calambokidis *et al.* 2000, Urbán-R *et al.* 2000).

Within Mexican waters, analysis of individual identification photographs (photo-ID) and mtDNA variation suggests further differentiation into subpopulations, with the humpbacks off Baja California (Baja) and mainland Mexico showing some isolation from those in the Revillagigedo Archipelago (Medrano-González *et al.* 1995, Urbán-R *et al.* 2000). However, Calambokidis *et al.* (2001) considered that Baja California could be a migratory corridor where whales from both the Revillagigedo Archipelago and mainland Mexico overlap. The preferred migratory destinations for humpbacks from mainland Mexico and Baja California appear to be the California-Oregon-Washington and BC summering regions (Urbán-R *et al.* 2000, Calambokidis *et al.* 2001). California is also a migratory destination for humpback whales wintering off Central America (Calambokidis *et al.* 2000). Although there have been some resightings of Revillagigedo humpbacks on summering grounds in California, British Columbia, and Alaska, the primary summering area for these animals remains unknown (Medrano-González *et al.* 1995, Urbán-R *et al.* 1999; 2000, Calambokidis *et al.* 2001, Witteveen *et al.* 2004). It has been suggested, based on acoustic detection of singing humpbacks and historical distribution, that the primary summer destinations of these animals are off the Aleutian Islands and/or the Bering Sea (Norris *et al.* 1999, Urbán-R *et al.* 2000).

In this study, satellite-monitored radio tags were deployed on humpback whales with the objective of investigating movements, migration routes, and feeding destinations of whales wintering near Socorro Island, Revillagigedo Archipelago, Mexico.

METHODS

Fieldwork took place at Socorro Island in the Revillagigedo Archipelago, Mexico, in February 2003. Humpback whales were tracked with Argos satellite-monitored radio tags deployed from a 6.5-m rigid-hulled inflatable boat. Tags were deployed with a modified air-powered system (Heide-Jorgensen *et al.* 2001) and placed as close to the whale's mid-dorsum as possible (*e.g.*, within 1 m forward of the dorsal fin).

Tags were designed for nearly complete implantation beneath the skin and consisted of a Telonics ST-15 UHF Argos transmitter and two Duracell 2/3 A lithium batteries housed in a stainless steel cylinder (19 cm long by 1.9 cm in diameter; see Mate *et al.* 2007 for details). Tags were programmed with a two-season duty cycle to prolong battery life, during which they transmitted for 4 h every day for the first 90 d (season one) and then for 4 h every other day thereafter (season two). During these transmission periods, the tags were capable of transmitting every 10 s when the tag was above water. A saltwater conductivity switch (SWS) established when the tag was underwater. Surfacing were determined when this SWS was above the surface of the water following a submergence of 6 s or more.

Tags were monitored by Argos Data Collection and Location Service receivers on NOAA TIROS-N weather satellites in sun-synchronous polar orbits. Locations were calculated by Argos from Doppler-shift data when multiple messages were received during the 7–16 min of a satellite's passage overhead. Argos assigns the following theoretical accuracies (of one standard deviation) to locations calculated when at least four messages are received during a satellite pass; Location Class1 (LC1): <1,000 m; LC2: <350 m; LC3: <150 m. These are considered high-quality locations. Argos does not assign an accuracy when less than four messages are received during a pass (LC0, A, B, Z). Based on results from previous tests (Mate *et al.* 1997), we assigned an 11.5-km error radius around these poor-quality locations.

Locations were edited using the assigned accuracies as radial errors. Locations on land farther than the assigned error distance from the ocean were not used. Poor-quality locations within 1 h of high-quality locations were not used. LC1 locations within 10 min of LC2 or LC3 locations were not used. If two poor-quality locations were less than 1 h apart, only the location providing the shortest distance between previous and subsequent acceptable locations was used. If two LC1 locations were <10 min apart, only the location providing the shortest distance between previous and subsequent acceptable locations was used. Minimum distances and speeds were then calculated between retained locations. Additional locations were eliminated if the speed between a location and the previous one was >15 km/h after adjusting for radial error. Lines connecting locations in figures represent the chronological order of locations, not necessarily the exact route taken by the whale.

Based on visual inspection of track lines, travel segments were classified as being in the wintering area, during migration, or in a feeding area. Whales were considered to have begun migration when their track took on a linear northwesterly direction, with little or no reverse movement and/or the animals moved northwest beyond the southern tip of Baja. Whales were considered to have reached a feeding area when they reached previously described feeding areas and their track ceased being linear.

Only high-quality locations were used to compute speeds due to the possibility of large errors in poor-quality locations. Additionally, location pairs had to be greater than a specified minimum interval apart to reduce the effect of errors in high-quality locations. The minimum allowable interval was determined by calculating mean speeds for both migratory and nonmigratory (wintering area, feeding area) travel segments and using the means to estimate the minimum times required (for each travel segment) for a whale to travel farther than the distance within the Argos accuracy range (1 km for each location or 2 km total). Based on these minimum times, we took a conservative approach and further filtered speeds by only using those for which the time between pairs of locations was greater than or equal to twice these minimum values.

Nonmigratory speeds were additionally filtered based on a maximum time period between pairs of locations. Because exact travel paths were unknown, distances calculated between locations far apart in time greatly underestimated an animal's true path, and as a result, also underestimated speed. We ran a regression analysis to examine the relationship between speed and time between high-quality nonmigration locations. We varied the maximum time in this analysis until we reached a point in which a significant relationship between speed and time between locations no longer existed. We then only looked at speeds between pairs of locations that were lower than the maximum time apart.

In addition to providing information for location calculation, the tags also provided a cumulative count of the number of surfacings the animal made. Surfacing rates

were calculated by dividing the number of surfacings between consecutive satellite passes by the elapsed time between these passes. Overall surfacing rates for each travel segment were calculated by dividing the total number of surfacings during a travel segment by the duration of that travel segment.

Both speed and surfacing rate were compared among the different travel segments. Data were tested for normality, equality of variances, and autocorrelation prior to statistical comparisons. Tests were considered statistically significant at a level of $P \leq 0.05$.

RESULTS

Eleven humpback whales were tagged between 6 and 17 February 2003, including five adults without calves, five mothers with calves, and one calf (Table 1). Eight of the tagged whales exhibited no reaction to the tagging process. The remaining three whales, including the calf, increased their swimming speed for a brief (≤ 3 min) period immediately after tagging.

Locations were acquired for all whales for periods ranging from 4.9 to 149.1 d ($\bar{x} = 59.3 \pm 46.1$ d). Data from the one adult that was tracked for less than 5 d (A5) were not included in further analyses. Total (minimum) distances traveled (calculated as the sum of rhumb-line distances between successive Argos locations) for the 10 whales tracked > 5 d ranged from 462 to 10,481 km ($\bar{x} = 4,212 \pm 3,322$ km, $n = 10$).

Movements

Eight whales left Socorro Island during their tracking period (Fig. 1). Mean time spent at Socorro before departure was 13.6 ± 9.3 d (range = 3.8–27.0 d). There was no difference in number of days before departure from Socorro (expressed as day of the year) between adults without calves ($\bar{x} = 63 \pm 12.1$ d, $n = 4$) and mothers with calves ($\bar{x} = 66 \pm 9.4$ d, $n = 4$, including the tagged calf; t -test $P = 0.73$).

Five of the tagged whales traveled to other known wintering areas within Mexico during their tracking periods (Fig. 1). Two of these whales (A4 and M6) traveled to both the mainland and the southern tip of Baja California whereas the remaining three (A1, A3, and MC3) went only to Baja California. After leaving Socorro Island, whale A4 spent approximately 4 d near the southern tip of Baja before heading to the mainland. Whale A4 then spent approximately 24 d off the Nayarit coast, visiting Banderas Bay as well as adjacent bays to the north. A mother with calf (M6) traveled to the Sinaloa coastline, just north of Mazatlán, spending approximately 12 d there. She then traveled to the southern tip of Baja, where she spent approximately 9 d before heading north.

Whales A1, A3, and MC3 spent approximately 3, 1, and 7 d, respectively, near the southern tip of Baja before heading north. Whale A1 also spent approximately 9 d at an area 130–350 km west-southwest of Magdalena Bay on the Baja California Sur coastline before continuing on its northward migration.

Seven whales were tracked moving north beyond the wintering areas in Mexico (Fig. 2). There was no difference in departure date from these areas (expressed as day of the year) between animals without calves ($\bar{x} = 89.3 \pm 15.9$ d, $n = 3$) and mothers with calves ($\bar{x} = 79.0 \pm 14.9$ d, $n = 4$, including the tagged calf; t -test $P = 0.42$). The northbound migration routes tended to be well offshore, with mean distance

Table 1. Deployment dates, number of days tracked, number of messages received, and summary statistics for 11 humpback whales tagged off Socorro Island, February 2003.

Tag number	Deployment date	Number of days tracked (days with locations)	Total distance (km)	Migration distance (km)	Mean \pm SD distance to shore (km) during migration	Total number of filtered locations (all quality/good quality)	Total number of locations used in speed calculations ^a	Overall surfacing rate per travel segment (surfacing per h)
A1	2/7/03	129.1	7,745	3,591	115 \pm 52.9	164/25	8	21mx 28mg 50bc
A2	2/8/03	26.1	1,132	n/a	n/a	36/4	0	26mx
A3	2/17/03	66.1	4,105	2,632 (partial ^b)	427 \pm 167.1	70/8	4	26mx 35mg
A4	2/17/03	71.2	6,558	3,009 (partial)	441 \pm 187.8	84/5	0	23mx 23mg
A5 ^c	2/10/03	4.9	222	n/a	n/a	2/2	0	— ^d
M1	2/6/03	23.1	553	n/a	n/a	12/2	0	27mx
M2	2/9/03	29.4	2,685	n/a	n/a	20/2	0	27mx
MC3	2/10/03	149.1	10,481	6,236	400 \pm 194.6	287/76	33	88mx 80mg 64ak
M4	2/15/03	23.2	462	n/a	n/a	34/14	8	34mx
M5	2/17/03	80.3	5,381	5,045 (partial)	935 \pm 348.4	110/24	16	40mx 42mg
M6	2/17/03	49.8	3,020	n/a	n/a	63/11	2	29mx 30mg
Mean \pm SD		64.7 \pm 44.7	4,212 \pm 3,322	—	444 \pm 256.6	80 \pm 83.4/ 15 \pm 21.7	6 \pm 10.2	—

Tag Number: A = adult, M = mother with calf, MC = calf and assumed accompanying mother. Travel Segment mx = Mexico, mg = migration, bc = British Columbia, ak = Alaska.

^a Only high-quality locations with further time interval filtering were used in speed calculations (see Methods for further detail).

^b Partial migration distance refers to tags that stopped transmitting before a whale reached a feeding ground.

^c A5 values not used in mean calculations.

^d Surfacing rate could not be calculated for this whale due to lack of data.

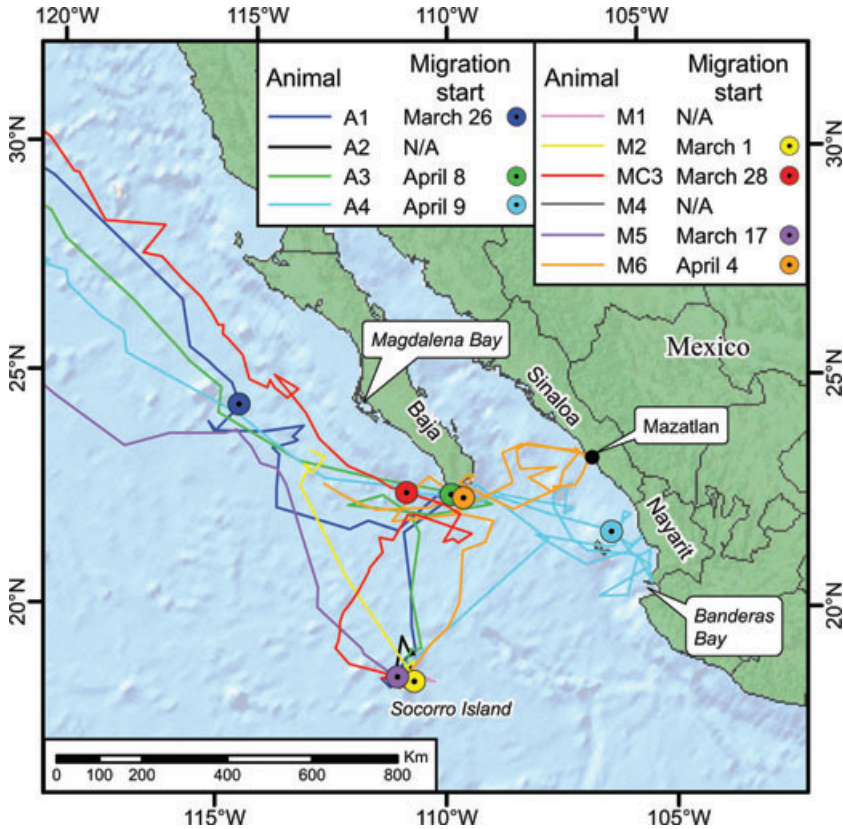


Figure 1. Satellite-monitored radio tracklines of 10 humpback whales tagged at Socorro Island, Mexico, in February 2003, showing movements within their wintering area. Projection used is North America Lambert Conformal Conic.

to shore being 444 ± 256.6 km for whales north of Magdalena Bay (25°N ; $n = 5$). Whale A1 traveled the closest to shore, coming within 41 km of Point Arena, California. Whales A3, A4, and M5 averaged courses of 310° , 307° , and 316° , respectively, during their migrations north. Calf MC3, assumed to be traveling with its mother throughout the entire tracking period, showed a similar course direction until it was off the Oregon coast. The final locations received for A3, A4, and M5 were 750 km off Point Conception, California, 1,040 km off Los Angeles, California, and 1,640 km off Tillamook, Oregon, respectively.

Whales A1 and MC3 were tracked to feeding grounds off British Columbia and Alaska, respectively (Fig. 3). Whale A1 arrived at the west coast of Vancouver Island, British Columbia on 27 April, 46 d after departing the southern tip of Baja (32 d after departing the area off Magdalena Bay). Total distance traveled during the migratory segment beyond Magdalena Bay was 3,591 km. Whale A1 spent 19 d along the edge of the continental shelf west of the central coast of the island, before making an excursion 135 km northwest along the shelf edge to an area off Kyuquot Sound. After approximately 6 d in this area, whale A1 headed southeast to an area 20 km off

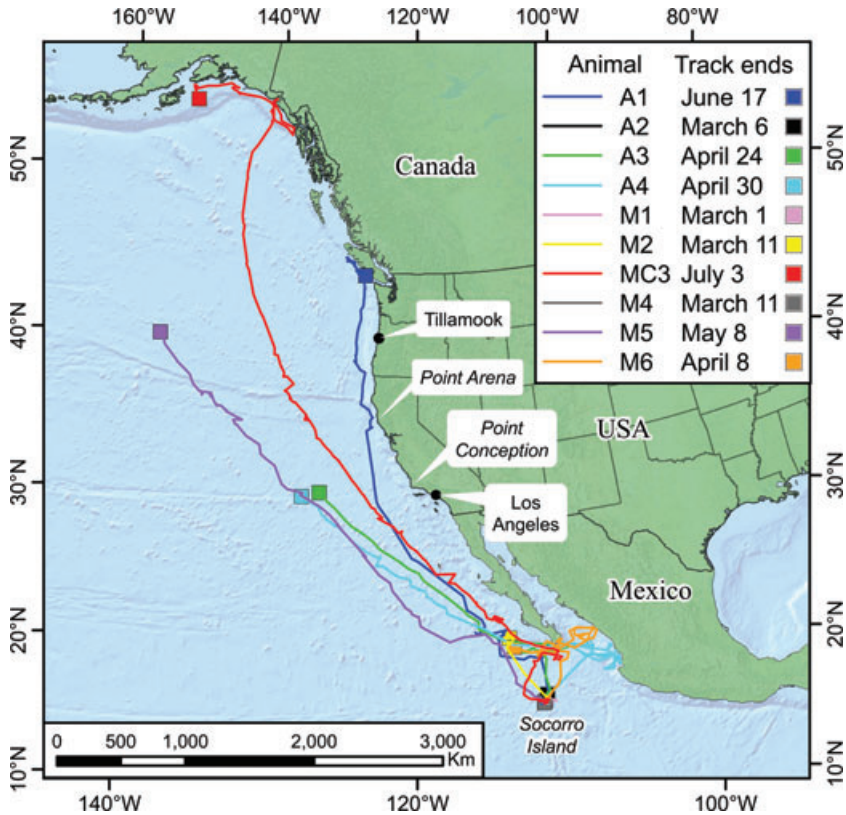


Figure 2. Satellite-monitored radio tracklines of 10 humpback whales tagged at Socorro Island, Mexico, in February 2003, showing full tracking periods. Projection used is North America Albers Equal Area Conic.

the entrance to Barkley Sound, where it spent the remainder of its tracking period (24 d).

Calf MC3 arrived in Yakutat Bay, Alaska, on 16 May, 49.1 d after departing the southern tip of Baja California on 28 March. The total distance traveled during this migration was 6,236 km. Four days later the calf/mother pair was at the northwest tip of Chichagof Island, where they remained for approximately 2 d. It then traveled for 20 d northwest along the Alaska coastline to Portlock Bank, an area approximately 130 km southeast of the tip of the Kenai Peninsula and 160 km west-northwest of Kodiak Island. The calf/mother pair remained in this area at least 30 d, until the end of its tracking period.

Speed

The mean speed between all high-quality locations during migration was 4.1 ± 2.3 km/h. Based on this value it would take a whale approximately 0.5 h to travel 2 km (the distance within the estimated accuracy range for Argos). Doubling this value restricted us to locations that were >1 h apart, resulting in a recalculated

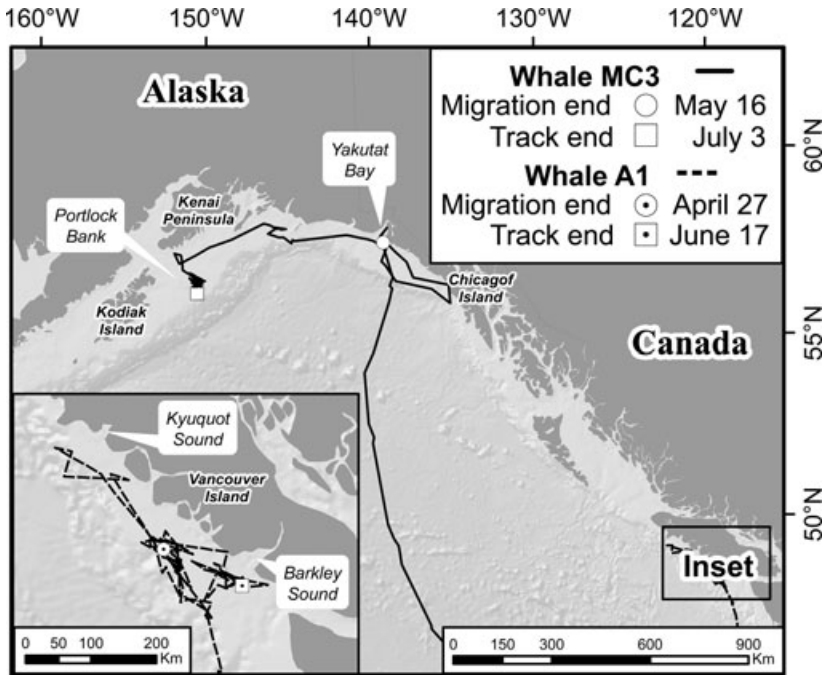


Figure 3. Feeding ground movements off Alaska for humpback whale calf MC3 tagged at Socorro Island, Mexico, on 10 February 2003; and off British Columbia (Inset) for humpback whale A1 tagged at Socorro Island, Mexico, on 7 February 2003. Projection used is North America Lambert Conformal Conic.

average migration speed of 4.0 ± 1.5 km/h (Table 2). Sample sizes were too small to permit a comparison of migration speeds between mothers with calves and adults without calves.

The mean speed between all high-quality locations during nonmigration travel was 1.3 ± 1.9 km/h. At this speed it would take a whale approximately 1.5 h to

Table 2. Mean speed between high-quality locations during wintering area, migration, and feeding area travel segments for humpback whales tagged off Socorro Island, Mexico, February 2003.

Tag number	Mean speed \pm SD (km/h) (<i>n</i>)		
	Wintering area	Migration	Feeding area
A1	N/A	2.8 ± 1.0 (6)	1.8 ± 1.0 (2)
A3	N/A	5.9 ± 0.3 (3)	N/A
MC3	2.1 ± 1.7 (5)	4.5 ± 1.8 (20)	2.7 ± 1.2 (6)
M4	1.0 ± 0.4 (7)	N/A	N/A
M5	N/A	2.8 ± 1.2 (15)	N/A
M6	0.6 (1)	N/A	N/A
Mean	1.2 ± 0.8 (3)	4.0 ± 1.5 (4)	2.2 ± 0.6 (2)

N/A means there were not enough high-quality locations to calculate speeds.

travel 2 km. Doubling this value gave us a minimum time between locations of 3 h. There was a significant negative relationship between speed and time between high-quality locations during nonmigration travel (linear regression slope $P = 0.006$, $r^2 = 6.93\%$). This relationship disappeared when time between locations was restricted to >3 h and <13 h. Therefore, nonmigration speeds were calculated only for high-quality locations that were >3 h and <13 h apart. Wintering area and feeding area speeds averaged 1.2 ± 0.8 km/h and 2.2 ± 0.6 km/h, respectively (Table 2).

Only whale MC3 provided enough data to allow speed comparisons among the three travel segments. Speeds were not autocorrelated within travel segments (Durbin-Watson $P = 0.27$), and were significantly higher during migration than for either wintering or feeding area travel segments for this calf (ANOVA $P = 0.01$).

Surfacing Rate

Overall surfacing rates ranged from 21 to 88 surfacings/h (Table 1) throughout the tracking periods. There was a significant negative relationship between surfacing rate and elapsed time between transmissions for whale A3 (linear regression slope $P = 0.02$, $r^2 = 4.0\%$). This relationship disappeared at elapsed times >1 h. Therefore, for consistency among whales, only surfacing rates calculated over elapsed times >1 h were used in analyses. To address autocorrelation, surfacing rates were further subsampled, keeping only those rates calculated for discrete day and night periods (resulting in elapsed times ranging from 3.6 to 11.2 h). To further standardize surfacing rates, we used only daytime values because our transmission schedule produced many more messages during the day than at night (no night values in many cases). Additionally, for the migration segment, we used only those values calculated from transmissions between 22.4°N and 34°N latitude, because migration pathways diverged greatly beyond those points.

Subsampling eliminated autocorrelation for all whales (Durbin-Watson $P = 0.95$) except A1 in the feeding area (Durbin-Watson $P = 0.02$). Because one of the two individuals that traveled to feeding areas presented autocorrelation, feeding area segments were not included in the comparison of surfacing rates between whales and travel segments. Five whales provided enough data to run a general linear model (GLM) comparison, for which there was a statistically significant relationship between surfacing rate and whales/travel segments (GLM $P < 0.001$; Fig. 4). Surfacing rates differed significantly between the calf (whale MC3) and all other whales, and between whales A1 and M5. Surfacing rates did not differ between wintering area and migration travel segments for any of the whales.

Two whales also provided enough data for feeding area comparisons. A natural log transformation was applied to surfacing rates for whale A1 to normalize the data and correct unequal variances between travel segments. Autocorrelation was corrected by the Cochrane-Orcutt procedure (Neter *et al.* 1989), using an r -value estimate of 0.60 (lag 1 residual value). Feeding area surfacing rate (mean = 48 ± 1.7 surfacings/h, $n = 16$) was significantly higher than wintering area (mean = 19 ± 2.7 surfacings/h, $n = 7$) or migration surfacing rates (mean = 23 ± 2.7 surfacings/h, $n = 7$) for whale A1 (ANOVA $P = 0.01$). The opposite pattern existed for whale MC3, which had a significantly lower surfacing rate in the feeding area (mean = 61 ± 8.1 surfacings/h, $n = 26$) than in the wintering area (mean = 73 ± 9.1 surfacings/h, $n = 14$) or during migration (mean = 75 ± 13.9 surfacings/h, $n = 8$; ANOVA $P = 0.0002$).

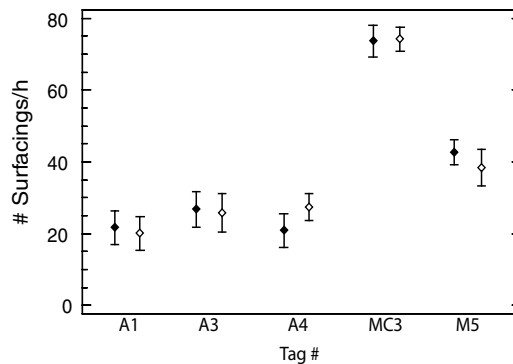


Figure 4. Least squares mean surfacing rates with 95% confidence intervals during migration (◆) and wintering (◇) travel segments for humpback whales tagged at Socorro Island, Mexico, February 2003.

Calf MC3 was the only whale that provided enough data to permit a diel comparison of surfacing rates. Such a comparison was only possible for the wintering area, as day length increased as the whale migrated north, providing even fewer nighttime messages. There was no autocorrelation in surfacing rates for calf MC3 (Durbin-Watson $P = 0.43$), which had higher surfacing rates at night ($\bar{x} = 108 \pm 3.0$ surfacings/h, $n = 11$) than during the day ($\bar{x} = 73 \pm 2.7$ surfacings/h, $n = 14$; ANOVA $P < 0.0001$).

DISCUSSION

Wintering Ground Movement

This study confirms the movement of humpback whales from Socorro Island to the Baja California coast and the Mexican mainland, calling into question the theory that Socorro humpbacks represent a separate subpopulation. Other studies, using both photo-identification and genetic evidence, have reported interchange of humpbacks between Baja and the Revillagigedos, but have stated that interchange with mainland Mexico is limited (Medrano-González *et al.* 1995, Urban-R *et al.* 1999, Calambokidis *et al.* 2001). Our study suggests that this interchange may not be as limited as previously thought, as two of the seven animals (28%) tracked beyond Mexican wintering areas visited the Mexican mainland.

Movement to the Mexican mainland was not restricted to one reproductive class, as both a mother/calf pair and an adult without a calf visited the area. They did not visit the same part of the mainland, however, which supports the suggestion by Salas (1993), as cited in Medrano *et al.* (1994) that the area between the mainland coast and Baja California may be favored by mother/calf pairs, whereas the coastal zone around Banderas Bay is favored by surface-active groups apparently involved in mating behavior. Although we do not know the behavior of whale A4 in this latter area, the animal was part of a surface-active group of six adults when tagged off Socorro Island.

Five of the seven whales that were tracked moving north visited the southern tip of Baja California. Calambokidis *et al.* (2001) suggest that Baja may represent a

migratory corridor, where whales from both the Revillagigedos and mainland Mexico overlap. Calambokidis *et al.* (2001) found that interchange of photographically identified humpback whales among Mexican wintering areas was most common between mainland and Baja, and only slightly lower between the Revillagigedos and Baja. Medrano-González *et al.* (1995) on the other hand, suggest that interchange between the Revillagigedos and Baja is low, based on significant differences in mtDNA haplotype frequencies between the two areas. A potential explanation for these differences is the distance offshore of most biopsy and photo-ID sampling. Biopsy samples used in the Medrano-González *et al.* (1995) study were obtained from an area (23°00'N and 109°30'W) 10 km offshore of the southeastern tip of Baja, although the closest any of the tagged whales came to shore in this area was 18 km. Perhaps animals migrating to/from the Revillagigedos represent an offshore component to humpback distribution around the southern end of Baja.

The area west-southwest of Magdalena Bay, where whale A1 spent approximately 9 d before continuing north, has been frequented on multiple occasions by satellite-tracked blue whales (Mate *et al.* 1999, Etnoyer *et al.* 2006). Etnoyer *et al.* (2006) suggest that the Baja California Frontal System, sometimes located off Magdalena Bay, is an important foraging habitat for turtles and whales. Concentrations of both euphausiids (*Euphausia pacifica*, *Thysannoessa gregaria*, and *Nematoscelis difficilis*) and pelagic red crabs (*Pleuroncodes planipes*) have been observed in this area (Brinton 1979). We hypothesize that whale A1 engaged in foraging activity during its time off Magdalena Bay. Opportunistic feeding behavior has been previously reported for humpback whales in Baja (Gendron and Urban-R 1993). Stopovers along the migratory route have also been reported for humpback whales: an individual tracked *via* satellite from Hawaii to Alaska in 1999 stopped for 38 d near the Kermit-Roosevelt Seamount (halfway between Hawaii and Alaska) during a time of increased productivity in the area (Mate *et al.* 2007).

Migratory Routes and Destinations

Migration routes for the tagged whales in this study were well offshore, averaging between 115 and 935 km from the coast. The five longest migrations had parallel routes up to 34°N, at which point one whale (A1) changed its course dramatically, coming close to shore before traveling to British Columbia. The calf/mother pair (MC3) changed course at the California/Oregon border to head to southeastern Alaska. The trajectories of the other three migrating whales suggest destinations farther west than for either whale A1 or MC3. It has been suggested that the primary destinations of humpback whales from the Revillagigedos are feeding areas in the offshore waters of the Gulf of Alaska and the Aleutian Islands, but that these animals are also seen, albeit in low numbers, off California, British Columbia, southeastern Alaska, Prince William Sound, and the Kodiak Island area (Urbán-R *et al.* 2000, Calambokidis *et al.* 2001). Our study suggests the latter areas, with the exception of California, may be more important than previously thought. The California, Oregon, and Washington area, on the other hand, does not seem to be a feeding destination for Revillagigedo humpback whales, as it is for humpbacks wintering in mainland Mexico (Urbán-R *et al.* 2000, Calambokidis *et al.* 2001). Whale A1 migrated within 41 km of the central California coast, but its final destination was not this area. Calambokidis *et al.* (2001) report seeing a Revillagigedo humpback off California, but we contend that the animal was likely in transit to a destination farther north.

A vast majority (91%) of tagged whale locations in feeding areas were greater than 15 km from shore, suggesting an offshore trend for Socorro humpbacks, which may explain their low photographic resight rates.

This study provides further evidence for the possibility of feeding ground overlap of humpback whales from Mexico with those from other North Pacific wintering areas. British Columbia is a feeding area used by humpbacks from all three Mexican wintering areas (Urbán-R *et al.* 2000), and in one case, by a humpback whale from Japan (Calambokidis *et al.* 2001). Photographic matches of whales have also been documented between Alaskan feeding areas and Mexican and Japanese wintering grounds (Urbán-R *et al.* 2000, Calambokidis *et al.* 2001, Witteveen *et al.* 2004), but the amount of summer overlap of whales from different wintering grounds is thought to be low. Southeastern Alaska, Prince William Sound, and Kodiak Island are feeding areas thought to be used primarily by humpback whales wintering in Hawaii (Baker *et al.* 1986, 1998; Calambokidis *et al.* 2001). Whale MC3 remained well offshore in these Alaskan areas, never getting closer than 17 km to the coast, so the extent of overlap with Hawaiian humpbacks feeding primarily near shore remains unknown.

Whale MC3 visited at least two previously described feeding areas (southeastern Alaska and Western Gulf of Alaska, including Prince William Sound) during the same summer. This is noteworthy because humpbacks in the North Pacific are thought to show strong site fidelity to feeding areas, with limited interchange among them (Baker *et al.* 1986, 1998; Waite *et al.* 1999; Calambokidis *et al.* 2001; Mizroch *et al.* 2004). Whether there are specific boundaries between these areas or a more continuous distribution with interchange decreasing with distance remains to be determined (Calambokidis *et al.* 2001). Waite *et al.* (1999) suggest the Kodiak Island region supports a separate feeding aggregation. It is unclear whether the Portlock Bank region identified in this study constitutes a distinct feeding area or is part of the Kodiak Island feeding area. Visitation of more than one feeding area in a single year may represent an unsuccessful search of areas where an animal experienced feeding success in a previous year. Subsequent visitations, within the same year, of likely successful feeding sites have been shown for other satellite-monitored humpback whales in southeastern Alaska and British Columbia, albeit on a smaller scale (Mate *et al.* 2007).

Migratory Distances and Speeds

The migration distances reported here for whales A1 (3,591 km) and MC3 (6,236 km) are similar to or greater than those previously reported for photo-identified humpbacks in the North Pacific (4,400 km by Gabriele *et al.* 1996, 1,900–5,322 km by Calambokidis *et al.* 2000) and satellite-monitored humpbacks in the South Atlantic (3,640 and 3,720 km by Zerbini *et al.* 2006). The distances reported for photo-identified whales represent minimum straight-line distances between end points, rather than a summation of distances between multiple locations, as for the satellite-monitored whales. The former would inherently be less than the latter. Using beginning and end points for the migrations documented in this study, the minimum straight line migration distances are more similar to those calculated from photo-identification studies (whale A1 = 2,908 km, whale MC3 = 4,718 km), representing 81% and 76% of the satellite-tracked migration lengths, respectively. Photo-identification studies in the South Pacific document much longer migration distances for humpback whales that cross the equator as they migrate

from feeding areas around the Antarctic Peninsula to wintering areas off Colombia (8,334 km, Stone *et al.* 1990) and Central America (8,299–8,461 km, Rasmussen *et al.* 2007).

Our observed migration speeds (ranging from 2.8 to 5.9 km/h) were similar to speeds reported for migrating humpback whales in the literature (4.74 km/h by Gabriele *et al.* 1996, 4.6, 4.6, and 6.2 km/h by Mate *et al.* 1998, 2.6 and 3.8 km/h by Zerbini *et al.* 2006, 2.5 km/h for singing whales and 4.0 km/h for nonsinging whales by Noad and Cato 2007). Speeds between high-quality locations were significantly greater during migration than during either wintering area or feeding area travel segments for the calf and assumed mother pair. Given that the exact route of travel between successive satellite locations is unknown, speeds based on the straight-line distance between these locations represent underestimates. This underestimation is likely higher for nonmigratory travel segments than for the more directional migratory travel segments. Nevertheless, we consider that our observations actually reflect the differences in speed between migratory and nonmigratory travel and coincide with previous satellite-telemetry studies. Mate *et al.* (1998) reported lower speeds for Hawaiian humpback whales during interisland travel (2.5 and 3.3 km/h) than for humpbacks migrating north from Hawaii (6.2, 4.6, and 4.6 km/h), but the calculations for each case were from different individuals. Zerbini *et al.* (2006) reported lower speeds for humpback whales on their feeding grounds in the Southwest Atlantic (0.75 and 1.00 km/h) than during migration (2.6 and 3.8 km/h). Slower speeds while in wintering or feeding areas are likely the result of movement patterns associated with breeding/nursing or foraging behavior, including searching for mates or food.

Surfacing Rates

A higher surfacing rate for the calf (whale MC3) than for all other tagged whales is not surprising given the fact that diving capability increases with body size (Schreer and Kovacs 1997). Surfacing rates for the calf were significantly lower, however, in the feeding area than in the wintering area or during migration. Whale MC3 would have been nursing throughout its tracking period. Lower surfacing rates over time likely represent increased diving ability (including longer dive durations) as the calf matured. Whale MC3 had a higher surfacing rate at night than during the day while in Mexico. The reason for this is unclear. If a higher surfacing rate is indicative of feeding, as was suggested for whale A1, perhaps the calf spent more time nursing at night. Feeding (by nursing calves or nonnursing animals) may be more costly, energetically, than other behaviors, and result in higher surfacing rates. Au *et al.* (2000) speculate that humpback whales are decreasing their surface-active behavior at night in favor of more acoustic signaling. Perhaps mothers are pursued less by males at night and have more undisturbed time for nursing. Resting near the surface may also result in higher surfacing rates if the tag's saltwater conductivity switch is frequently exposed to the air.

Higher surfacing rates for whale A1 in the feeding area compared to those in the wintering area or during migration are also not surprising because feeding is energetically expensive for lunge-feeding rorquals (Acevedo-Gutiérrez *et al.* 2002). Accurate surfacing rate information is critical for accurate abundance estimation using cue-counting methods (Hiby 1992). Surfacing rate information may also be important in assessing whales' reactions to human disturbance (Richardson *et al.*

1995). Therefore, it is important to know that surfacing rates may change depending upon behavior, location, or development (for calves).

ACKNOWLEDGMENTS

This study was funded by the National Oceanic and Atmospheric Administration Ocean Explorer's program (contracts AB133F-02-SE-1428 and AB133F-03-SE-1471) and by donors to the Oregon State University Endowed Marine Mammal Program. The study was conducted under a permit issued by the Secretaría de Medio Ambiente y Recursos Naturales, Mexico (permit SGPA/DGVS 00512). The Oregon State University Institutional Animal Care and Use Committee approved this research. We thank G. Booth, T. Follett, and M. L. Mate for assistance in the field. We thank T. Follett for map preparation and A. Weiss for distance-to-shore calculations. The manuscript was greatly improved by comments from C. S. Baker, L. Irvine, J. Estes, A. Aguilar, and two anonymous reviewers.

LITERATURE CITED

- ACEVEDO-GUTIÉRREZ, A., D. CROLL, AND B. TERSHY. 2002. Feeding costs limit dive time in large whales. *Journal of Experimental Biology* 205:1747–1753.
- AU, W. W. L., J. MOBLEY, W. C. BURGESS, M. O. LAMMERS AND P. E. NACHTIGALL. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Marine Mammal Science* 16:530–544.
- BAKER, C. S., L. M. HERMAN, A. PERRY, W. S. LAWTON, J. M. STRALEY, A. A. WOLMAN, G. D. KAUFMAN, H. E. WINN, J. D. HALL, J. M. REINKE AND J. OSTMAN. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Marine Ecology Progress Series* 31:105–119.
- BAKER, C. S., L. MEDRANO-GONZALEZ, J. CALAMBOKIDIS, A. PERRY, F. PICHLER, H. ROSENBAUM, J. M. STRALEY, J. URBÁN-RAMIREZ, M. YAMAGUCHI AND O. VON ZIEGESAR. 1998. Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. *Molecular Ecology* 7:695–707.
- BRINTON, E. 1979. Parameters relating to the distributions of planktonic organisms, especially euphausiids, in the eastern tropical Pacific. *Progress in Oceanography* 8:125–189.
- CALAMBOKIDIS, J., G. H. STEIGER, K. RASMUSSEN, J. URBÁN-R., K. C. BALCOMB, P. LADRÓN DE GUEVARA, M. SALINAS-Z., J. K. JACOBSEN, C. S. BAKER, L. M. HERMAN, S. CERCHIO AND J. D. DARLING. 2000. Migratory destinations of humpback whales that feed off California, Oregon and Washington. *Marine Ecology Progress Series* 192:295–304.
- CALAMBOKIDIS, J., G. H. STEIGER, J. M. STRALEY, L. M. HERMAN, S. CERCHIO, D. R. SALDEN, J. URBÁN-R., J. K. JACOBSEN, O. VON ZIEGESAR, K. C. BALCOMB, C. M. GABRIELE, M. E. DAHLHEIM, S. UCHIDA, G. ELLIS, Y. MIYAMURA, P. LADRÓN DE GUEVARA-P., M. YAMAGUCHI, F. SATO, S. A. MIZROCH, L. SCHLENDER, K. RASMUSSEN, J. BARLOW AND T. J. QUINN, II. 2001. Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17:769–794.
- ETNOYER, P., D. CANNY, B. R. MATE, L. E. MORGAN, J. G. ORTEGA-ORTIZ AND W. J. NICHOLS. 2006. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography* 53:340–358.
- GABRIELE, C. M., J. M. STRALEY, L. M. HERMAN AND R. J. COLEMAN. 1996. Fastest documented migration of a North Pacific humpback whale. *Marine Mammal Science* 12:457–464.
- GENDRON, D., AND J. URBÁN-R. 1993. Evidence of feeding by humpback whales (*Megaptera novaeangliae*) in the Baja California breeding ground, Mexico. *Marine Mammal Science* 9:76–81.

- HEIDE-JØRGENSEN, M.-P., L. KLEIVANE, N. ØIEN, K. L. LAIDRE AND M. V. JENSEN. 2001. A new technique for deploying satellite transmitters on baleen whales: Tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. *Marine Mammal Science* 17:949–954.
- HIBY, L. H. 1992. Fin whale surfacing rate as a calibration factor for cue-counting abundance estimates. *Report of the International Whaling Commission* 42:707–709.
- MATE, B. R., R. GISINER AND J. MOBLEY. 1998. Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. *Canadian Journal of Zoology* 76:863–868.
- MATE, B. R., B. A. LAGERQUIST AND J. CALAMBOKIDIS. 1999. Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. *Marine Mammal Science* 15:1246–1257.
- MATE, B., R. MESECAR AND B. LAGERQUIST. 2007. The evolution of satellite-monitored radio tags for large whales: One laboratory's experience. *Deep-Sea Research II* 54:224–247.
- MEDRANO-GONZÁLEZ, L., A. AGUAYO-LOBO, J. URBÁN-RAMÍREZ AND C. S. BAKER. 1995. Diversity and distribution of mitochondrial DNA lineages among humpback whales, *Megaptera novaeangliae*, in the Mexican Pacific Ocean. *Canadian Journal of Zoology* 73:1735–1743.
- MEDRANO, L., M. SALINAS, I. SALAS, P. L. DE GUEVARA, A. AGUAYO, J. JACOBSEN AND C. S. BAKER. 1994. Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering grounds of the Mexican Pacific Ocean. *Canadian Journal of Zoology* 72:1711–1774.
- MIZROCH, S. A., L. M. HERMAN, J. M. STRALEY, D. A. GLOCKNER-FERRARI, C. JURASZ, J. DARLING, S. CERCHIO, C. M. GABRIELE, D. R. SALDEN AND O. VON ZIEGESAR. 2004. Estimating the adult survival rate of central north pacific humpback whales (*Megaptera novaeangliae*). *Journal of Mammalogy* 85:963–972.
- NETER, J., W. WASSERMAN AND M. H. KUTNER. 1989. *Applied linear regression models*. Richard D. Irwin, Inc., Homewood, IL.
- NISHIWAKI, M. 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whale marking results. Pages 171–191 in K. S. Norris, ed. *Whales, dolphins, and porpoises*. University of California Press, Berkeley and Los Angeles, CA.
- NOAD, M. J., AND D. H. CATO. 2007. Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science* 23:481–495.
- NORRIS, T. F., M. McDONALD AND J. BARLOW. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *Journal of the Acoustical Society of America* 106:506–514.
- RASMUSSEN, K., D. M. PALACIOS, J. CALAMBOKIDIS, M. T. SABORÍO, L. D. ROSA, E. R. SECCHI, G. H. STEIGER, J. M. ALLEN AND G. S. STONE. 2007. Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biology Letters* 3:302–305.
- RICHARDSON, W. J., C. R. GREEN, JR., C. I. MALME AND D. H. THOMSON. 1995. *Marine mammals and noise*. MMS Contract 14–12-0001–30673; LGL report TA994. Available from LGL Ltd., King City, Ontario, Canada.
- SALAS, I. V. R. 1993. Intervalos de reproducción y tasas de nacimiento de las ballenas jorobadas (*Megaptera novaeangliae*) identificadas en dos áreas de reproducción del Pacífico Mexicano, 1986–1991. Professional thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D. F. 97 pp.
- SCHREER, J. F., AND K. M. KOVACS. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* 75:339–358.
- STONE, G. S., L. FLOREZ-GONZALEZ AND S. KATONA. 1990. Whale migration record. *Nature* 346:705.
- URBÁN-R., J., C. F. ALVAREZ, M. Z. SALINAS, J. JACOBSEN, K. C. BALCOMB, III, A. L. JARAMILLO, P. LADRON DE GUEVARA P AND A. L. AGUAYO. 1999. Population size of humpback whale, *Megaptera novaeangliae*, in waters off the Pacific coast of Mexico. *Fishery Bulletin* 97:1017–1024.
- URBÁN-R., J., A. JARAMILLO L., A. AGUAYO L., P. LADRÓN DE GUEVARA P., M. SALINAS Z., C. ALVAREZ F., L. MEDRANO G., J. K. JACOBSEN, K. C. BALCOMB, D. E. CLARIDGE,

- J. CALAMBOKIDIS, G. H. STEIGER, J. M. STRALEY, O. VON ZIEGESAR, J. M. WAITE, S. MIZROCH, M. E. DAHLHEIM, J. D. DARLING AND C. S. BAKER. 2000. Migratory destinations of humpback whales wintering in the Mexican Pacific. *Journal of Cetacean Research and Management* 2:101–110.
- WAITE, J. M., M. E. DAHLHEIM, R. C. HOBBS, S. A. MIZROCH, O. VON ZIEGESAR-MATKIN, J. M. STRALEY, L. M. HERMAN AND J. JACOBSEN. 1999. Evidence of a feeding aggregation of humpback whales (*Megaptera novaeangliae*) around Kodiak Island, Alaska. *Marine Mammal Science* 15:210–220.
- WITTEVEEN, B. H., J. M. STRALEY, O. VON ZIEGESAR, D. STEEL AND C. S. BAKER. 2004. Abundance and mtDNA differentiation of humpback whales (*Megaptera novaeangliae*) in the Shumagin Islands, Alaska. *Canadian Journal of Zoology* 82:1352–1359.
- ZERBINI, A. N., A. ANDRIOLO, M. P. HEIDE-JØRGENSEN, J. L. PIZZORNO, Y. G. MAIA, G. R. VANBLARICOM, D. P. DEMASTER, P. C. SIMÕES-LOPES, S. MOREIRA AND C. BETHLEM. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the southwest Atlantic Ocean. *Marine Ecology-Progress Series* 313:295–304.

Received: 27 June 2007

Accepted: 28 March 2008